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SHORTER ARTICLES AND DISCUSSION

MODIFYING FACTORS AND MULTIPLE ALLELOMORPHS IN RELATION TO THE RESULTS OF SELECTION

In the prevailing controversy as to the effectiveness of selection, those who reject such effectiveness put forth *multiple modifying factors* as the explanation of the results observed. The given character (for example, the coat color in Castle's hooded rats) is held to depend on one main factor (determining the presence or absence of the character) and upon numerous modifying factors; the number of the latter present in a given case determines the degree of expression of the character. Selective breeding is then held to act, as it does with relation to all other Mendelian factors, merely by making diverse combinations of such factors. Many are gathered together in certain individuals, few in others, and the degree of expression of the inherited character varies accordingly.

Much evidence is presented that this is actually the mode of operation in many cases where selection is effective. Thus are explained the visible results of selection in Castle's rats; thus the unexpected fact that many of the mutations of *Drosophila* have shown themselves (in accordance with Castle's prediction) to be amenable to selection, although in other respects they behave like alterations of a single unit factor. This is indeed the usual explanation for that effectiveness of selection which is coming to light in so many cases; and in many of the cases it appears clear that the explanation is correct.

But in which direction does this explanation carry us? To answer this question we must know what these multiple modifying factors are. If they are mere examples of the static condition of diversity observed among so many closely related organisms, the answer falls in the negative direction, so far as the effectiveness of selection in accumulating actual alterations of hereditary characters is concerned. But if they should themselves turn out to be the actual alterations of hereditary constitution that are accumulated by selection, then the answer confirms the effectiveness of selection and adds greatly to our knowledge of how it is brought about. What are the facts?

For these we may turn to the organism of which the genetics are best known; to the fruit fly *Drosophila;* and we may accept the accounts presented by those most uncompromising opponents of the effectiveness of selection, the investigators of *Drosophila* in the Columbia laboratory. Their account we cannot suspect of being colored to favor the selectionist point of view. We find data as to certain known modifying factors in the recent important paper of Bridges (1916) on "Non-Disjunction of the Chromosomes in *Drosophila.*" Bridges tells us that he has found no less than seven diverse factors that modify the single primary grade of eye color known as eosin. These seven factors are located in parts of the chromosomal apparatus different from the spot on which the presence or absence of eosin depends, and each is inherited in Mendelian fashion. One of these factors lightens the eosin color in a fly with eosin eyes, nearly or quite turning eosin to white; this factor Bridges calls "whiting." Another has the effect of lightening the eosin color a little less, giving a sort of cream color; this is called "cream *b.*" A third factor dilutes the eosin color not so much; it is called "cream *a.*" In addition to these, Bridges tells us that he has discovered three other diluters of the eosin color; we will call them the fourth, fifth and sixth diluters. And finally Bridges tells us of another factor whose only effect is to make eosin darker; this factor he calls "dark." We get therefore the following list of the modifying factors for eosin color:

1. Whiting
2. Cream *b*
3. Cream *a*
4. Fourth diluter
5. Fifth diluter
6. Sixth diluter
7. Dark

We have then in *Drosophila* minutely differing conditions of a single shade of color, brought about by seven modifying factors. Concerning these, Bridges makes the following remark, which is worthy of particular attention:

> A remarkably close imitation of such a multiple factor case as that of Castle's hooded rats could be concocted with the chief gene eosin

for reduced color, and these six diluters which by themselves produce no effect, but which carry the color of eosin through every dilution stage from the dark yellowish pink of the eosin female to pure white (Bridges, 1916, p. 149).

Thus we see that in *Drosophila* we could get the same sort of graded results that Castle does with his rats, only in *Drosophila* this is by multiple modifying factors, whereas Castle believes that in the rat it is by actual alterations in the hereditary constitution!

But what are these modifying factors? And here we come to the astonishing point. *These modifying factors are themselves alterations in the hereditary constitution!* Bridges leaves no doubt upon this point. He lists and describes them specifically as mutations; as actual changes in the hereditary constitution.

Now so far as I can see, the question involved in the selection controversy is as to the occurrence of minute changes in the hereditary constitution, and their accumulation by selection; so that by selection various grades of a given external character can be obtained. In *Drosophila,* according to Bridges, such changes occur; changes which give, so far as our present imperfect knowledge goes, at least seven diverse grades of a single tint (that is itself, as we shall note, only one grade in another series of seven known grades). By means of these graded changes one could obtain, by the mutationist's own statement, the continuously graded visible results which selection actually gives. Is not then the controversy as to the effectiveness of selection at an end?

As to just where the graded hereditary changes occur there remain indeed certain differences of opinion; some selectionists, like Castle, hold that the various grades of a given external character are due to diverse minute modifications of the same unit character—of the same locus in the chromosome; while, as we have seen, the modifying factors are due to changes in diverse parts of the hereditary material. This matter of detail does not touch the main point, but it is of interest to ask what the work of the mutationists gives us on this question. It is curious to find that their studies of *Drosophila* furnish almost all that could be asked by the radical selectionist as to the existence of a single unit character in a series of numerous hereditary gradations. The best instance here is again the color of the eye, which furnished us also our example of modifying factors. The color eosin, of which the modifying factors give us seven grades, is itself only one of another series of seven grades that are due to diverse alterations in the same unit factor—in the same chromosomal locus. As we know from the studies of *Drosophila,* this locus is a certain region of the X-chromosome. When this locus retains its normal condition the eye is red. Some years ago a variation was observed by which the eye lost its red color, becoming white. Somewhat later another variation came, by which the eye color became eosin. By the wonderfully ingenious methods which the advanced state of knowledge of the genetics of *Drosophila* has made possible, it was determined that the mutations white and eosin are due to changes in a particular part of a particular chromosome, and that indeed the two are due to different conditions of a particular region of the X-chromosome. In other words, they show different conditions of the same unit. Moreover the normal red represents a third condition of this same unit.

Later a fourth condition of this same unit was found, giving a color which lies nearer the red, between the red and eosin; this new color was called cherry. We have now four grades of this single unit character.

And now, with the minute attention paid to the grades of eye color, new grades begin to come fast. In the November number of *Genetics,* Hyde (1916) adds two new grades, one called "blood," near the extreme red end of the series; the other, called "tinged," near the extreme white end; in fact, from the descriptions, it requires careful examination to distinguish these two from red and white respectively. So we have now six grades of this unit. And in the same number of the same journal, Safir (1916) adds another intermediate grade, lying between tinged and eosin; this he calls "buff."

So, up to date we know from the mutationists' own studies of *Drosophila* that a single unit factor presents seven gradations of color from white to red, each grade heritable in the usual Mendelian manner. These grades or "multiple allelomorphs" as they are called, are the following:

1. Red
2. Blood
3. Cherry
4. Eosin

5. Buff
6. Tinged
7. White

Three of these seven grades have been made known to us within the last six months. It would not require a bold prophet to predict that as the years pass we shall come to know more of these gradations, till all detectable differences of shade have been made out and each shown to be inherited as a Mendelian unit. Considering that the work on *Drosophila* has been in progress but eight or nine years, we have already remarkable progress toward a demonstration that a single unit character may present as many heritable grades as can be distinguished; that the grades may give a pragmatically continuous series. This is precisely the situation that the selectionist postulates.

Furthermore, as we have seen, besides this primary series of seven grades, due to alterations of a single unit factor, there is a secondary series containing seven more grades, all affecting the central grade (eosin) of this primary series, but due to alterations of other parts of the germinal material. How much more does the selectionist require?

This situation in *Drosophila* is not exceptional. To mention one or two other examples, Castle and Wright (1916) find a large series of such diverse conditions of a single factor (''multiple allelomorphs'') determining various shades of coat colors in rodents. Emerson (1917) in his recent account of the extraordinary condition of affairs in the genetics of pericarp colors in corn, talks of ''a series of not less than nine or ten multiple allelomorphs,'' which moreover leap back and forth from one condition to another in bewildering fashion.

To sum up, it appears to me that the work in Mendelism, and particularly the work on *Drosophila,* is supplying a complete foundation for evolution through the accumulation by selection of minute gradations. We have got far away from the old notion that hereditary changes consist only in the dropping out of complete units, or that they are bound to occur in large steps. The ''multiple allelomorphs'' show that a single unit factor may exist in a great number of grades; the ''multiple modifying factors'' show that a visible character may be modified in the finest gradations by alterations in diverse parts of the germinal material. The objections raised by the mutationists to gradual change through selection are breaking down as a result of the thoroughness of the mutationists' own studies.

The positive contribution of these matters to the selection problem is to enable us to see the important rôle played by Mendelism in the effectiveness of selection. Hereditary variations, such as give rise to the multiple allelomorphs and multiple modifying factors, occur in some organisms rather infrequently, as measured by the time scale of human happenings. If there were no interchange of factors among individuals and stocks, it would take a long time to obtain in one individual all the six diluters of the eosin color of the *Drosophila* eye; one arises in one individual, another in another. But by selective crossbreeding it is possible to bring together into one stock all the modifiers that have been produced in diverse stocks. Mendelism acts as a tremendous accelerator to the effectiveness of selection.

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A WING MUTATION IN PIOPHILA CASEI

IN the early part of December, 1915, I began to breed the "cheese skipper" *Piophila casei,* in order to see if mutations were to be found in this fly. The source of my stock was a small piece of Italian cheese containing a dozen or so larvæ.[1] As these were doubtless the offspring of one female, inbreeding has been very close. Up to June 22, 1916, only one heritable mutation had been found among the thousands of individuals bred; this was the wing defect described below, which was first noted on March 12, 1916.

[1] This work was carried on at the Osborn Zoological Laboratory, Yale University, New Haven, Connecticut. It was in New Haven that I obtained the cheese. Contribution No. 135, Zoological Laboratory, University of Texas.